

## Butterfly Taxonomy: A Reply

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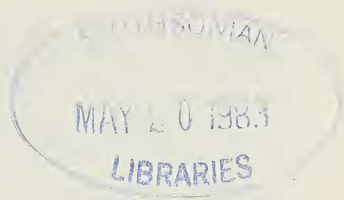
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Our *Catalogue/Checklist* (Miller and Brown, 1981) is an updating of that prepared by Dyar (1903), which in turn was taken generally from that by Skinner (1898). The promised catalogue that was to follow dos Passos (1964) was not forthcoming, and our publication attempted to fill this gap. It is an up-to-date (through 1979) revision of the nomenclature which 1) follows an order acceptable to taxonomists of worldwide background (this often differs from the arrangements in popular books and more parochial works); 2) follows the best and most recent revisions of genera (including the recognition as genera of taxa previously recognized as subgenera); 3) considers higher taxa on their worldwide complement of species, not just those from the Nearctic; 4) takes into account biological and ecological advances in knowledge, such as different foodplant preferences that separate distinct, but previously overlooked genera; and 5) attempts to follow the *International Code of Zoological Nomenclature*. The *Catalogue/Checklist* does not take into consideration political constraints or the aspects of continued usage of incorrect, frequently employed names. Should the conservation of these names be desired, the place to apply for their reinstatement is the International Commission on Zoological Nomenclature.

It should be clearly stated here that no new names, at the generic or other level, have been employed by Miller and Brown (1981). In every case, the generic names are ones proposed validly by earlier authors. There are 669 notes which provide detailed information (often in telegraphic form because of space constraints) on authorities followed and, at least by implication, reasons for changes from pre-existing nomenclature.

Such a treatment as ours is not made without objections, and those complaints made by Ehrlich and Murphy (1982) require some objective replies. Their points are by no means new—similar reactions have followed every reclassification that has appeared. The catalogue format precludes detailed explanation of every change (though such changes are documented elsewhere in the literature); Ehrlich and Murphy's com-



plaints likewise are unsupported by specific explanations. The usual objections to nomenclatorial changes are: old, reliable, comprehensive genera are being split; the literature will be adversely affected by "wholesale name changes"; the new names do not reflect relationships, obscuring the affinities of species that "everyone knows belong together"; and that in general taxonomists are meddlesome creatures who keep themselves busy changing names for the sake of changing them for no biological purpose.

Attacks like those mentioned may be seen in the pages of Strecker (1876: 118-120) berating Scudder (1875), of Holland (1931: 325) and Forbes (1960) in their not accepting the work of Lindsey, Bell and Williams (1931), by Hovanitz (1962: 95-96) in his criticism of dos Passos and Grey (1947) and again by Hovanitz (1965: 18) regarding dos Passos (1964). In the latter critique, Hovanitz states, "Names proposed by splitters do not have to be used merely because they have been proposed." He did *not*, however, go so far as to suggest that these names be expunged from the literature.

We are being criticised essentially for being "out of touch" with modern systematic work, but are we? We had expected a certain amount of controversy to arise when the classical treatment of the Papilionidae by Munroe (1961) was expanded. This expansion was not done solely on the basis of the genitalia, as suggested by Ehrlich and Murphy (1982); rather the morphology of all life stages was considered along with biological parameters such as foodplant preferences. Munroe never claimed to have *all* of the answers for the Papilionini, and the passage from his work quoted by Ehrlich and Murphy indicates that he had questions about his ability to find differences within "*Papilio*", differences which have become apparent with more life history data. Our treatment, like that of Eliot (1978), generally follows the outline of Munroe's classification, but at a different level.

Each of the papilionid genera that we accepted is either a lauraceous, rutaceous or umbelliferous feeder (the main exception being *Papilio*, *s. str.*, which contains some rutaceous feeders, apparently as a response to competition by congenors). Ferris and Emmel (1982) studied the rutaceous feeding *P. polyxenes color* W. G. Wright and showed that while it feeds in the wild on Rutaceae, its larvae actually do better on Umbelliferae, but it is out-competed for the umbellifers by the very successful *P. zelicaon* Lucas. This switching of foodplant groups within a phyletic line is interesting and may be of fundamental biological and systematic importance. While there are some biochemical similarities between a number of Umbelliferae and some Rutaceae, *they are not biochemically identical!* Berenbaum (1981) shows how narrowly *Papilio*, *s. str.*, is tied to plants (chiefly Umbelliferae) with concentrations of furanocoumarins, and he further shows that rutaceous feeders within that genus also will utilize Umbelliferae that

contain these substances.

Perhaps the most characteristic furanocoumarin-bearing rutaceous plant is *Citrus*, the host of *Heraclides* and *Priamides*. This strongly indicates that these genera are sister groups of *Papilio* (perhaps *Priamides*, despite its structural dissimilarities, is a good subgenus of *Heraclides*), and that this cluster of genera is evolutionarily very different from the lauraceous feeders. Among Nearctic swallowtails, the lauraceous feeders are the ones Miller and Brown (1981) include in *Pterourus*.

These genera are not so restricted in numbers ("one species per genus") as a parochial examination of them would indicate. *Papilio* is found throughout the northern hemisphere and contains at least twice as many species as are represented in the Nearctic. *Heraclides* is a genus of at least 15 Nearctic and Neotropical species, *Priamides* contains at least ten species from the Neotropics and *Pterourus* has eight or more Nearctic and Mexican representatives. Further, while all are bird-lime mimics in early larval instars, only *Heraclides* and *Priamides* retain this character in later stadia. *Pterourus* larvae in later instars are green with thoracic "eye-spots", presumably as a sham defense, and mature *Papilio* larvae are conspicuously banded with green and black totally unlike other groups. The osmeterium of *Papilio* is shorter and stubbier than that of *Heraclides* and *Pterourus*. Thus, the statements by Ehrlich and Murphy (1982) about the division of "*Papilio*" by Huebner [1819] are merely their way of setting up "straw men" so that they could knock them down. In a much quieter way, we did the synonymization of these names to one another, and the fact that perhaps Huebner established genera for the wrong reasons or otherwise faultily cannot diminish that he *did* establish them.

Other examples could be cited, such as the objections to the division of "*Lycaena*" into constituent genera (Sibitani, 1974; Miller and Brown, 1979), but some of the comments made by Ehrlich and Murphy (1982) suggest that they did not really read these papers for content, only to find grounds for criticism.

Further criticism is rendered because we have "ignored perfectly good subgenera" and raised them to generic standing. This may be true, perhaps, but the steps were taken for reasons entirely different from the capriciousness attributed to us. Subgeneric names, *if consistently applied*, can indeed carry great taxonomic and evolutionary information. The difficulty is that most advocates of subgenera are not consistent. Thus, we have a situation analagous to that demonstrated by Eliot (1978: 121) where members of the genus *Euploea* Fabricius are tabularly divided into subgenera, which taxa are not mentioned again in the text. The "use" of subgenera in this way conveys little or no information about specific groupings, and *Euploea* is left as an apparently homogeneous assemblage of related species. Division of *Euploea* into separate genera (note that we are *not* advocating it), elevated from subgeneric standing and placed into a



well-defined hierarchical classification, does not obfuscate relationships, but rather, it strengthens them.

In North American butterflies, good candidates for demotion to subgeneric standing would include *Occidryas*, *Hypodryas*, *Abaeis*, *Pyrissitia*, *Falcapica* and *Priamides*, and we would then recommend reinstatement of at least the subgenera *Semnopsyche* and *Erynnides*. Nevertheless, while Ehrlich and Murphy admit the at least "weak subgeneric" status of *Occidryas*, they steadfastly refuse to refer to "*Euphydryas (Occidryas) editha* (Boisduval)", preferring a strict binominal designation. We could certainly accept *consistent* use of subgenera, but not the sporadic usage of taxonomic names at whatever level.

The arguments put forth on scientific *vs.* vernacular names are, we feel, specious and clearly irrelevant in the context of the rest of their paper. Much the same must be said about the thoughts expressed on species-level taxonomy. We shall comment neither on the correctness nor the political morality of the thoughts expressed by Ehrlich and Murphy (1982) on the reasons for naming subspecies, save to state that there are other thoughts on the matter.

It cannot be questioned that evolutionary problems are more complex than are reflected in the pages of popular texts: if they were not more complex, they would have been solved long ago. Perhaps Ehrlich and Murphy are correct when they accept the concept of the evolutionary unimportance of subspecies (Wilson and W. Brown, 1953), but acceptance of that idea also suggests that the detailed study of even smaller demes (for example, the *Occidryas editha* studies of Ehrlich and his coworkers) may not be entirely or even mostly evolutionary in nature. Gould (1982: 104) states unequivocally, "We cannot learn everything we need to know about evolutionary trends by studying what happens within demes, if only because species can act as units of selection." The key word in this quotation is "everything", and the key thought is that no one study contains *all* of the information needed to pass evolutionary judgments.

Another point that Ehrlich and Murphy (1982) seem to have forgotten is that evolution is a *dynamic* process, so it is natural that some taxa will be "better" (*i. e.*, phyletically more divergent from other taxa) than others. Were evolution a static process, phenetic measures might show similarities and gaps, but since taxa are in varying stages of divergence, phenetic analysis does not always show relationships correctly. Within taxonomic lines, some taxa are diverging more rapidly, others less, than their closely related counterparts. Whether one accepts classical gradualism, the punctuated equilibrium theory of Eldredge and Gould (1972) and Gould and Eldredge (1977) or something that embodies parts of both theories, it is clear that taxon "A" might well evolve, by one means or another, faster or slower than taxon "B".

We object to formalization of the generic nomenclature in Howe (1975)

chiefly because that book is replete with errors (Ferris, 1976) and because the nomenclature is at odds with that recognized by specialists throughout the world. Similarly, we must also reject the attempt to formalize the higher classification of Ehrlich (1958) and Ehrlich and Ehrlich (1967): that particular proposal is self-serving. Our argument with the Ehrlich schema is not necessarily with the arrangement of taxa (we more or less agree), but rather, with the taxonomic levels in which the categories are placed. The statement (Ehrlich, 1958) that his classification was somehow more in line with those adopted in other insect orders was not convincingly defended; nor did that classification take into account what is known about fossil butterflies simply because so many of the relevant examples have been discovered in the last two decades. Many of these fossils indicate slower, a few faster, rates of evolution than would be indicated by the five to eleven million years' duration for invertebrate species given by Raup (1978) and Stanley (1979). Gould (1982:95) suggests, however, "...some species may survive longer than others because they inhabit a certain kind of environment, not because their morphologies are 'better' in any conventional sense." Again, we must reiterate that the last word has not been written on butterfly higher classification or phylogeny.

This reply is essentially a plea for additional research, unfettered by concerns about "sacred cows". We were somewhat loath to write this article, but the mere suggestion of the suppression of Miller and Brown (1981) by Ehrlich and Murphy (1982) left us with no alternative. We reject their call for censorship, wondering to what other papers it ultimately might be applied: science is the censor, not individual scientists or editors.

In the Editor's Note preceding Miller and Brown (1981), C. V. Covell, Jr., states, "No arrangement of taxa has yet proved to be the 'right' one, and we expect the years and the gristmill of scientific discourse to bring us closer to a true phylogenetic classification of the Lepidoptera." Our work was written in that spirit, and we welcome the renewed interest in taxonomic investigation that we hope it spurs. It is only through such research that progress can be made.

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